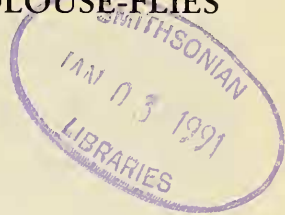


A PHYLOGENETIC ANALYSIS OF THE WOODLOUSE-FLIES (DIPTERA, RHINOPHORIDAE)

by

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ABSTRACT

The Rhinophoridae are redefined on the basis of the apomorphic structure of the aedeagus. Evidence is provided for the exclusion of four genera, viz., *Angioneura* Brauer & Bergenstamm, 1893, *Melanomyia* Rondani, 1856, *Morinia* Robineau-Desvoidy, 1830, and *Termitoloemus* Baranov, 1936; all four are transferred to the Calliphoridae. The genera of Rhinophoridae are analyzed phylogenetically with the aid of the results of the present investigation and the sparse information available on the morphology of the larval stages. The structure of the aedeagus provides several set-defining characters and the aedeagus of many species is depicted for the first time. *Cirillia* Rondani, 1856, is proposed as a synonym of *Phyto* Robineau-Desvoidy, 1830.

INTRODUCTION

Within the calyptrate flies the species with a row of bristles on the meron (hypopleuron) constitute a well-corroborated monophyletic group, the Tachinoidea (Tachinidae sensu Girschner (1893), Calliphoroidea sensu Hennig (1958), Tachinidae (sensu lato) sensu Griffiths (1972), or Oestroidea sensu McAlpine et al. (1981)). Most recent authors, including the present, accept five major groups in the Tachinoidea, viz., Oestridae (sensu lato), Calliphoridae, Sarcophagidae, Tachinidae, and Rhinophoridae. Although Crosskey (1965) restricts the name Tachinoidea to the Calliphoridae, Sarcophagidae, Tachinidae, and Rhinophoridae, synapomorphies not shared by the Oestridae (which would be their sister group), to my knowledge have not been provided for these four families by any author.

The family Stackelbergomyiidae Rohdendorf, 1948, was obviously established because no evidence for incorporating the single aberrant species into any of the existing families could be found. An investigation by Herting (1981) suggests that it should be included in the Tachinidae. More interesting are the Neotropical Mesembrinellinae (Calliphoridae). Crosskey (1965) is of the opinion that an improved classification of the Tachinoidea (in his definition as given above) would result if "peculiar groups such as Mesembrinellinae were treated as families" (p. 43). Guimarães (1977) follows this recommendation and raises the group to family status: Mesembrinellidae, founding his decision on five

"consistent differences" between Mesembrinellinae and the remaining Calliphoridae. These differences corroborate the monophyly of the Mesembrinellinae, but the Calliphoridae sensu Guimarães are characterized solely on sympleisomorphies and fail to support a family status of the Mesembrinellinae. An argument for splitting up the Calliphoridae would be that the simple, non-opercular lappet of the mesembrinelline metathoracic spiracle is plesiomorphic, as this would separate the Mesembrinellinae (still monophyletic) not from the Calliphoridae but from all other Tachinoidea, the monophyly of which would be corroborated by their opercular metathoracic spiracle. This may be the reason for Crosskey's (1965: 43) note that the Mesembrinellinae "may not be Tachinoidea at all".

I hesitate to place the Mesembrinellinae as sister group to all other Tachinoidea and prefer to treat them as Calliphoridae. The structure of the mesembrinelline aedeagus with strong, forwardly curved dorsolateral processes (paraphalli) seems a reasonable synapomorphy with the Calliphoridae (and perhaps with the Rhinophoridae?).

A small digression may be made here, brought about by the recent (and past) disagreement of family status criteria. Some authors, e.g., Steyskal (1974) and Hackman & Väisänen (1982), have mentioned the inconsistency of Griffiths' (1972) splitting of the Muscidae sensu Hennig (1958, 1965) into Muscidae and Fanniidae when he unites all tachinoid flies in a single family: Tachinidae (sensu lato).

However, although Hennig (1965) states that: "Eine der sichersten Feststellungen, vielleicht die gesichertste, die man über das phylogenetische System der Muscidae treffen kann, ist die, dass zwischen den Fanniinae auf der einen Seite und der Gesamtheit aller übrigen Muscidae... ein Schwestergruppenverhältnis besteht" (p. 9), he does not bring conclusive evidence of the monophyly of the "Muscidae sensu lato". Therefore, a separation is to be preferred. If the tachinoids are considered a monophyletic group, they are best treated in common when used for outgroup comparison, and the formal rank — whether family or superfamily — is of minor importance in a phylogenetic sense. Only the ranking of the group relative to the other Calyptratae is important as this constitutes a phylogenetic hypothesis.

The monophyly of the Tachinoidea seems fairly corroborated. Griffiths (1972) mentions the following synapomorphies with respect to the groundplan of the Calyptratae:

- (1) hypopleuron with strong bristles below metathoracic spiracle,
- (2) eighth sternum (♀) entire,
- (3) vein m_{1+2} sharply bent towards r_{4+5} apically,
- (4) anal vein not reaching wing margin,
- (5) sixth tergum (♂) shortened, less than half as long as 5th tergum,
- (6) eighth tergum vestige (♂) lost.

The loss of the "eighth tergum vestige" in males is based on a questionable interpretation of a median ventral sclerotization in the postabdomen of some Anthomyiidae and Scatophagidae (Griffiths, 1972: fig. 61); this sclerotization more likely is a secondary acquisition.

Another character which may be autapomorphic to the Tachinoidea is:

- (7) lappet of metathoracic spiracle divided, posterior lappet shaped as an operculum.

This opercular metathoracic spiracle, absent in all other calyptrates, is present in the majority of the Tachinoidea; the non-opercular metathoracic spiracle present in the Mesembrinellinae and a few other Calliphoridae, some groups of Tachinidae, Macronychiinae of the Sarcophagidae, almost all Rhinophoridae, and many Oestridae (sensu lato) may be secondarily derived.

The sister group relations of the Tachinoidea within the Calyptratae are still largely unsolved, and the characters mentioned by Griffiths are not necessarily autapomorphies for the Tachinoidea, viz., items 4 and 5 mentioned above,

which also occur among other calyptrate groups. A shortened anal vein (A_1) is characteristic of both the Muscidae and Fanniidae. A few genera in the Tachinoidea (e.g., some Oestridae (sensu lato) and Tachinidae, *Bengalia* Robineau-Desvoidy in the Calliphoridae) possess an extended anal vein, a character which both Hennig (1958) and Griffiths (1972) consider to be secondary. It is interesting, however, that Andersen (1982) reports aerial swarming of male *Siphona* Meigen as the first example within the Tachinidae and suggests (Andersen, 1982, 1983) that an extended anal vein may be assignable to the groundplan of the Tachinidae (and then possibly to all the Tachinoidea).

The shortened abdominal tergum 6 in males is of general occurrence in the Muscidae and Anthomyiidae as well.

The Rhinophoridae are typical members of the Tachinoidea as defined above (fig. 1), but the affinities to other tachinoid families are still unclear. Many earlier authors placed the rhinophorids with the blow-flies and flesh-flies in a Calliphoridae (sensu lato), but in a phylogenetic sense this constitutes an entirely unacceptable non-group arising by the splitting off of the flies possessing a swollen subscutellum — the Tachinidae. Mesnil (1939) derived most of the subfamilies of Tachinidae from different rhinophorid stocks, thereby rendering the Rhinophoridae paraphyletic (and the Tachinidae polyphyletic), but at present most authors give the Rhinophoridae family rank, acknowledging their uniqueness and the present lack of evidence for a closer relation to any of the other tachinoid families. Kugler (1978), and especially Crosskey

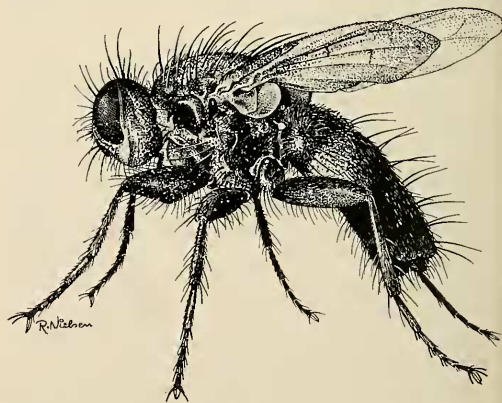


Fig. 1. *Stevenia deceptoria* (Loew); a typical woodlouse-fly.

(1977), give a more detailed review of previous differences of opinion regarding the family affinities.

LARVAL BIOLOGY AND MORPHOLOGY

Although the family is small, an unambiguous demarcation of the Rhinophoridae has not been possible. This is due in part to the existence of deviating tropical forms, e.g., *Bequaertiana* Curran, and in part to an external morphology intermediate between that of typical calliphorids and typical tachinids. More important, however, is the lack of information concerning the morphology and biology of the larval stages. All known first-stage larvae possess a distinctive cephalopharyngeal skeleton with the anterior part of the pharyngeal sclerite greatly elongated and with two or more teeth on the dorsal arc of the mandibles — evidently synapomorphic characters. The larval habit of parasitizing woodlice (Isopoda) is likewise unique to the Rhinophoridae, and interesting insofar as very few biological relationships between Diptera and Crustacea are known (see Roubaud, 1903; Mercier, 1921; Oldroyd, 1964, and Burger et al., 1980).

Only seven genera of rhinophorids actually have been recorded as woodlouse parasites, viz., *Stevenia* Robineau-Desvoidy, *Tricogena* Rondani, *Rhinophora* Robineau-Desvoidy, *Melanophora* Meigen, *Paykullia* Robineau-Desvoidy, *Phyto* Robineau-Desvoidy, and *Cirillia* Rondani (note that *Cirillia* is a synonym of *Phyto*, see discussion below). Specific host records for the Palaearctic species are given by Herting (1961) with supplements in Kugler (1978). Parker (1953) mentions breeding of the introduced *Melanophora roralis* (Linnaeus) in Brazil. No host records exist for any of the Nearctic, Afrotropical, or Oriental species.

There has been some doubt as to whether the Rhinophoridae could be parasites in invertebrates other than isopods, and the tendency has been to disregard any such record. Obviously, the report of *Melanophora helicivora* Goureux being bred from the gastropod *Helicella conspurcata* (Draparnaud) is based on a mis-identification. As judged from the description and drawings (Goureux, 1843: figs. 1, 2), the species does not belong to *Melanophora* at all, but may be a calliphorid.

Lundbeck (1927) mentions a specimen of *Melanophora roralis* bred from egg-cocoons of the spider *Araneus cornutus* Clerck. I have seen this specimen, a female deposited in the Zoological Museum, Copenhagen, and it is correctly identified by Lundbeck.

In addition to this there are several reports of rhinophorids parasitizing insects (table 1), and it is probable that rhinophorids occasionally (accidentally?) may parasitize arthropods other than isopods.

Very little has been written on the morphology of the larvae of the woodlouse-flies. Thompson (1934) treated in detail the larval stages of eight species, viz., *Paykullia maculata* (Fallén), *Phyto angustifrons* (Rondani), *Phyto discrepans* (Pandellé), *Phyto melanocephala* (Meigen), *Melanophora roralis*, *Stevenia atramentaria* (Meigen) (as species B), *Tricogena rubricosa* (Meigen), and *Rhinophora lepida* (as species A). However, Thompson obtained all his material from dissections of woodlice as most of his attempts to obtain eggs from female flies caught in the wild and hatch these to first-instar larvae failed. Furthermore, he often assumed that rhinophorid larvae from a single colony of woodlice were conspecific. This has resulted in some erroneous identifications in his earlier works (Thompson, 1917, 1920; corrected in 1934:

Table 1. List of non-isopod hosts of the Rhinophoridae.

parasite/predator	specimens	host	reference
<i>Melanophora roralis</i>	1 ♀	eggs of <i>Araneus cornutus</i> Clerck (Araneae)	Lundbeck (1927)
	?	? <i>Pyrallis farinalis</i> (Linnaeus) (Lepidoptera, Pyralidae)	Bezzi & Stein (1907)
<i>Stevenia umbratica</i>	?	<i>Callidium violaceum</i> Linnaeus (Coleoptera, Cerambycidae)	Bezzi & Stein (1907)
<i>Rhinophora lepida</i>	1 ♂	<i>Paranthrene tabaniformis</i> (Rottemburg) (Lepidoptera, Aegeriidae)	Kolubajiv (1962)
	1 ♂	<i>Saperda carcharias</i> (Linnaeus) (Coleoptera, Cerambycidae)	Kolubajiv (1962)
<i>Rhinomorinia sarcophagina</i>	1 ♂, 1 ♀	<i>Malacosoma neustria</i> (Linnaeus) (Lepidoptera, Lasiocampidae)	Kolubajiv (1962)

380). Of the first-instar larva of *Phyto angustifrons* Thompson had only a single defective specimen (the cephalopharyngeal skeleton and a skin fragment). The depicted cephalopharyngeal skeleton (Thompson, 1934: pl. 19, fig. 47) is of the heavy, sclerotized type found in *Stevenia*, *Tricogena*, and *Rhinophora* and very unlike the cephalopharyngeal skeleton of *Paykullia*, *Melanophora*, and other species of *Phyto*.

The first-stage larva assigned to *Phyto angustifrons* probably belongs to another species (very likely a *Stevenia*). The cephalopharyngeal skeleton of the second- and third-stage larva of *P. angustifrons* (Thompson, 1934: pl. 20, figs. 48, 56) is more in accordance with that of *Phyto* species.

Bedding (1973), in an extract of his Ph. D. thesis, described eggs and larval stages of all English species — actually the same species as those described by Thompson (1934) except for *P. angustifrons*. The larvae, especially first instars, possess several features which are very useful in a phylogenetic context, but at present the larval stages are known for only a small fraction of the species described. In addition, the uniqueness of many of the features makes any outgroup comparison almost inapplicable in the distinction between apomorphic versus plesiomorphic larval characters within the family.

The first-stage larvae known at present comprise two distinct groups (see figs. 8—44 in Bedding, 1973):

A. *Phyto*, *Paykullia*, *Melanophora*

- (1) mandibles with normal degree of sclerotization, with three or more small teeth on the dorsal arc,
- (2) elongated anterior part of pharyngeal sclerite with an incision,
- (3) setal bases unmodified,
- (4) posterior end of larva highly modified for supporting the larva in erect posture; with a dorsal tongue, terminal sac-like lobes, and ventral ridges.

B. *Stevenia*, *Tricogena*, *Rhinophora*

- (1) mandibles heavily sclerotized, with two strongly developed teeth,
- (2) elongated anterior part of pharyngeal sclerite without an incision,
- (3) setal bases protruded into proleg-like structures,
- (4) posterior end of larva simple, with inflated ventral vesicles.

Bedding notes that the two morphologically distinct groups of first-stage larvae possess differences in their biology (referring to a paper (in

prep.) which unfortunately has not yet been published).

The toothed mandibles of the first-stage larvae are probably an adaptation for penetrating the body wall of the host, analogous to the serrate median tooth of tachinid larvae which enter the host through a strongly sclerotized cuticle (Clausen, 1940: fig. 210 A). This character is clearly an autapomorphy for the Rhinophoridae as toothed mandibles occur very sporadically in other Tachinoidea, e.g., the warblefly of the lechwe antelope (Howard, 1980).

The two types of cephalopharyngeal skeleton can not be separated into an apomorphic and a plesiomorphic state at present; indeed, it is possible that both types are apomorphic with respect to the groundplan of the Rhinophoridae, but this may be the least parsimonious solution to the problem.

The proleg-like setal bases must be considered an apomorphic character as these are absent in the majority of the Tachinoidea and nothing indicates their suppression in other rhinophorids. This character is found in *Stevenia*, *Tricogena*, and *Rhinophora* and may be a synapomorphy of the *Stevenia* group (see discussion below), thereby corroborating the monophyly of this group.

The two types of modified posterior end of the first-stage larva present a problem somewhat analogous to that of the cephalopharyngeal skeleton. However, until more information on the sister group relations of the Rhinophoridae within the Tachinoidea becomes available, it is reasonable to assume that the sister group possesses first-stage larvae with unmodified posterior ends. The terminal lobes, the dorsal tongue, and the free, posteriorly oriented ventral ridges will then be apomorphic characters, and the terminal lobes will be the apomorphic homologues of the inflated vesicles. This will corroborate the hypothesis that *Paykullia*, *Phyto*, and *Melanophora* are part of a monophyletic group (the *Phyto* group) not containing *Stevenia*, *Tricogena*, or *Rhinophora*.

RECOGNITION OF THE RHINOPHORIDAE

Crosskey (1977: 7) gives an excellent discussion of the status and recognition of the family, but he admits that his recognition couplet does not ensure a certain identification. A further complication is the recently described genus *Baniassa* Kugler. This genus has a well-developed metathoracic opercular spiracle, but the absence of a distinct operculum has hitherto

provided one of the most important single characters for rhinophorid recognition. Besides the structure of the metathoracic spiracle, the characters most helpful in recognizing the family have been the tongue-shaped or oval lower calypteres which are widely removed from the scutellum, the bend of vein M which never is greatly concave, and the combination of bare prosternum, proepisterna, greater ampullae, postalar walls, laterotergites, and supra-squamal ridges.

In the majority of the Tachinoidea the structure of the aedeagus (and other structures of the terminalia) provides important characters in the diagnostic segregation of species and is often used in the construction of evolutionary trees and in the definition of taxonomic categories above the species level. Some illustrative examples are the works of Mueller (1926) on the Tachinoidea, Roback (1954) on the Sarcophaginae, Verbeke (1962) on the Tachinidae, Kurahashi (1966) on the Luciliinae, Lehrer (1970) on the Calliphoridae, and Lehrer (1973) on *Sarcophaga* (sensu stricto). The distiphallus of male rhinophorids, however, is seldom depicted, not even in the revisions of the Palaearctic (Herting, 1961) and Afrotropical (Crosskey, 1977) species, and the information stored in this structure is largely unknown. Mueller (1926) made an early attempt to construct a "Stammbaum... auf Grund der Penisform" of the Tachinoidea, but only a few rhinophorids were included and the drawings are more or less incorrect. Séguy (1941) made a preliminary division of the Rhinophoridae (as a subfamily of the Calliphoridae, sensu lato) into four groups on the basis of the male genitalia, but he dissected only a few representatives and his definition of the (sub)family included several tachinid, sarcophagid, and calliphorid genera.

The structure of the aedeagus may provide additional characters to be used in the recognition of the family; and in order to use this structure in a redefinition of the family and in the reconstruction of the phylogeny at the generic level, the following hypothetical groundplan of the tachinoid aedeagus is accepted (terminology as in Hennig, 1976 and McAlpine et al., 1981) (fig. 2).

Like most other calyptrate flies a well-developed basiphallus, distiphallus and epiphallus are present. The distiphallus is more or less tubular, somewhat swollen basally, and possesses spinules on the ventral surface. The distiphallus is connected to the sclerotized basiphallus by

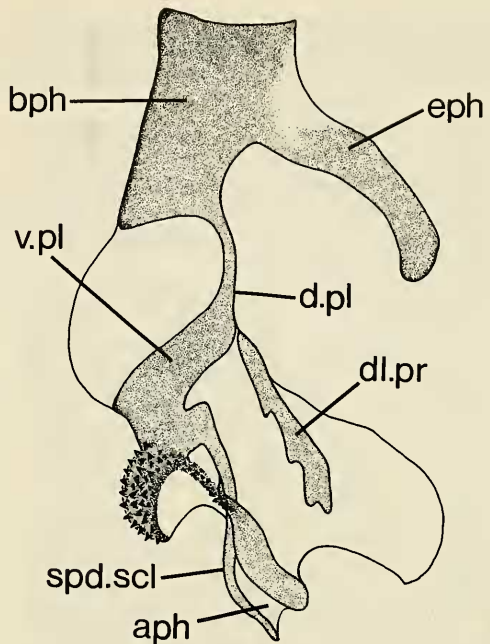


Fig. 2. *Stevenia atramentaria* (Meigen); aedeagus, lateral view. Abbreviations: aph = acrophallus, bph = basiphallus, d.pl = dorsal plate, dl.pr = dorsolateral processes, eph = epiphallus, spd.scl = spermduct sclerotization, v.pl = ventral plate.

means of the dorsal plate, which divides distally into a pair of dorsolateral processes. The dorsal plate is extended ventrally on each side, forming two ventral plates. The acrophallus, carrying the phallotreme, is a simple, membranous extension of the distiphallus, probably encircling the three openings of the female spermathecal ducts during copulation.

The aedeagus of many rhinophorids, e.g., *Phyto* spp. (figs. 15, 16), has not diverged markedly from this ancestral state, and the view is in agreement with that of Rikhter (1980), who mentions an epiphallus, basiphallus, a distiphallus immovably connected to the basiphallus, and "relatively" simple structure of distiphallal parts as the groundplan of the Tachinidae.

Two features of the rhinophorid aedeagus deserve mention. A possible autapomorphy for the Rhinophoridae is the well-developed ventral plates clearly set off from the dorsal plate and fused along the ventral margins, thus forming a sclerotized ring. Only the genus *Paykullia* possesses unfused, but closely apposed, ventral plates, and this may be considered a reversal, as discussed below. It may seem somewhat odd to

attach any importance to this character considering the enormous variability of the distiphallus within the Tachinoidea, and certainly it is possible to enumerate several cases of non-rhinophorids (especially among the Calliphoridae) with fused ventral plates. However, most or all of these instances will be easily rejected as convergencies and I think the distinctive ventral plates will be of great value in the proper recognition of any rhinophorid.

The other character to be mentioned is the sclerotization of the ventral part of the spermduct extending from the ventral plates to the phallotreme. In *Phyto* and *Parazamimus* this sclerotization is interrupted basally and does not reach the ventral plates (figs. 14—16). All other rhinophorid genera possess a sclerotization fused to the ventral plates and continuing to the phallotreme.

The use of outgroup comparison for assessing the level at which this character is apomorphic is difficult to apply as the sister group of the Rhinophoridae is unknown. A similar spermduct sclerotization is of general occurrence in the Calliphoridae (the mesohypophallic sclerotization of Salzer (1968)) but absent in most Sarcophagidae and Tachinidae. If the interrupted spermduct sclerotization of *Phyto* is considered to be plesiomorphic within the Rhinophoridae then *Phyto* must be the sister group to all other genera. This hypothesis seems falsified by the several synapomorphies in the imaginal morphology of *Phyto* and *Baniassa*, and by the apomorphic larval morphology of *Phyto*, which is also found in *Paykullia* and *Melanophora*. Probably the possession of a spermduct sclerotization fused to the ventral plates is a ground-plan character in the rhinophoridae, and the spermduct sclerotization may be an important argument for a close affinity to the Calliphoridae.

To sum up, the characters which I regard as the most useful in the recognition of the family are the following:

Larval characters:

- (a) cephalopharyngeal skeleton of first-stage larvae with toothed mandibles and elongated pharyngeal sclerite,
- (b) parasites of woodlice.

Imaginal characters:

- (c) aedeagus with well-developed ventral plates that are fused (or closely apposed) along the ventral margins,
- (d) lower calypteres tongue-shaped, diverging from the scutellum,

- (e) metathoracic spiracle without a distinct operculum (except in *Baniassa*),
- (f) prosternum, proepisterna, greater ampullae, postalar walls, laterotergites, and suprasqual ridges bare,
- (g) bend of vein M never greatly concave.

It is important to note that the characters given not necessarily are rhinophorid autapomorphies as some of them are found in other tachinoids as well. Character (f) is obviously plesiomorphic within the Tachinoidea and is provided to facilitate the exclusion of rhinophorid-like Calliphoridae.

GENERA MISPLACED IN THE RHINOPHORIDAE

The previous lack of an unambiguous definition of the family has resulted in some moving about of a few genera. Crosskey (1977) in his review of the Rhinophoridae gives evidence for the exclusion of genera like *Shannoniella* Townsend (Tachinidae), *Bezzimyia* Townsend (Tachinidae), and *Opsodexia* Townsend (Calliphoridae), all of which earlier have been considered to belong to the Rhinophoridae (or to the Rhinophorinae as a subfamily of the Tachinidae). This exclusion is accepted in the present paper and only the genera listed by Crosskey (1977), with the additions of Kugler (1978), will be treated in detail. Some of these clearly deviate from the definition given above and ought to be excluded from the Rhinophoridae.

Angioneura Brauer & Bergenstamm.

Angioneura has long been treated as belonging to the Rhinophoridae, but North American authors, especially Downes (1955, 1965), have transferred it to the Calliphoridae, this view being accepted by Wood (1979). Crosskey (1977) discusses this genus in the paragraph "included genera possibly not Rhinophoridae" but accepts its rhinophorid status. It is noteworthy that the genus *Angioneura* contains some species with enlarged lower calypteres, viz., *A. obscura* (Townsend), the only Nearctic species seen, and *A. acerba* (Meigen). The lower calypteres of the other species investigated, although distinctly diverging from the scutellum, are semicircular and not of the typical tongue-like shape characteristic of the Rhinophoridae.

The larvae, still unknown from the first stage, seem to be parasites of snails rather than woodlice. Two of the five Nearctic species of *Angioneura* are recorded as having been bred from snails (Reinhard, 1929; Downes, 1965) and *A. cyrtoneurina* (Zetterstedt) from the Palaearc-

tic Region has been bred from the snail *Succinea elegans* Risso (Čepelák & Rozkošný, 1968). Bedding (1973) collected thousands of woodlice from about 50 localities in southern England in order to breed all native species of Rhinophoridae. He did not, however, obtain any specimens of *A. acerba* or *A. cyrtoneurina*, the only English representatives (Kloet & Hincks, 1976). On this evidence I find it highly unlikely that any species of *Angioneura* parasitizes woodlice.

The presence of species with enlarged or semicircular lower calypteres, the life habit of the larvae as parasites in snails, and the ventral plates of the distiphallus which, although rather well-developed, are completely free of and widely removed from each other (fig. 3), clearly corroborate the exclusion of *Angioneura* from the Rhinophoridae, and I follow Downes (1965) in regarding *Angioneura* as a calliphorid.

It is interesting that the exclusion of *Angioneura* leaves the American continent without indigenous species of rhinophorids. Two species, however, have been established on this continent, both probably introduced from Europe: *Phyto discrepans*, which occurs in southern Canada, and *Melanophora roralis*, which is recorded from southern Canada, the eastern United States, the West Indies (Jamaica, St. Thomas), and Brazil.

Examined species: *Angioneura acerba* (Mei-

gen, 1838), *A. cyrtoneurina* (Zetterstedt, 1859), *A. fimbriata* (Meigen, 1826), *A. obscura* (Townsend, 1919).

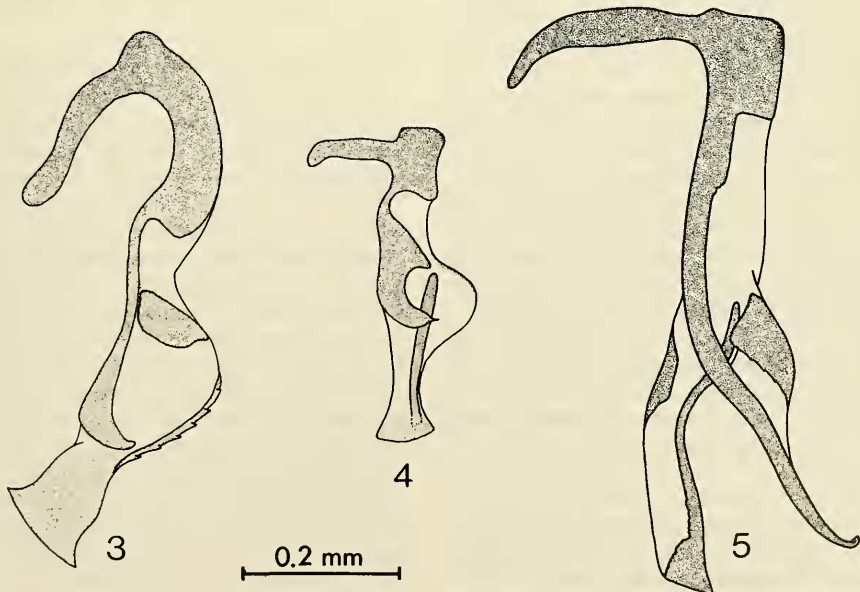
Melanomya Rondani.

This genus is apparently closely related to *Angioneura*, and Downes (1965) treats *Angioneura* as a subgenus of *Melanomya*. No host records are known for the single European species, *Melanomya nana* (Meigen), but as with *Angioneura*, the absence of any specimens of *Melanomya nana* in the material studied by Bedding (1973) reduces the probability of a woodlouse parasitizing habit. In addition, the ventral plates of the distiphallus are rather widely separated (fig. 4).

The similarity to *Angioneura* will then indicate a position in the Calliphoridae.

The metathoracic spiracle of *M. nana* differs from the typical, somewhat triangular, rhinophorid type of spiracle (Crosskey, 1977: figs. 41—44) in being broad with a well-developed anterior fringe. This may provide further evidence for a calliphorid status as the majority of the Calliphoridae possess a rather large metathoracic spiracle, most often with a distinctly enlarged anterior lappet.

Examined species: *Melanomya nana* (Meigen, 1826).



Figs. 3—5. Aedeagus of Calliphoridae, lateral view: 3, *Angioneura fimbriata* (Meigen). 4, *Melanomya nana* (Meigen). 5, *Morinia melanoptera* (Fallén).

Morinia Robineau-Desvoidy.

This genus is accepted as belonging to the Rhinophoridae by Crosskey (1977) in spite of the presence of distinct hairs on the postalar walls, a character used by Crosskey to exclude rhinophorid-like Calliphoridae. Haired postalar walls occur in many Calliphoridae and in the subfamily Sarcophaginae of the Sarcophagidae (very seldom in subfamily Miltogramminae), but I have not found this trait in any tachinid or rhinophorid.

The presence of haired postalar walls and the lack of well-developed ventral plates (fig. 5) make an inclusion under the Rhinophoridae somewhat improbable. Two other characters that may corroborate an exclusion are the well-developed metathoracic spiracular operculum (although an operculum is present in a single rhinophorid genus) and the presence of a weakly developed facial carina, these characters being most conspicuous in the Japanese species *M. nigerrima* (Herting). A facial carina is not found in any rhinophorid but occurs frequently in the Calliphoridae and Tachinidae. On this sparse evidence I find a position in the Calliphoridae most corroborated.

Examined species: *Morinia melanoptera* (Fallén, 1810), *M. nigerrima* (Herting, 1961).

Termitoloemus Baranov.

The only known species, *T. marshalli* Baranov, was originally described as belonging to the tribe Bengaliinae in the Calliphoridae. This was based on a similarity in life habits between *Bengalia* and *Termitoloemus*, predators of ants and termites, and similarities in the structure of the proboscis and palpi. Sabrosky & Crosskey (1970) transferred *Termitoloemus* to the Rhinophoridae because of the possession of a simple metathoracic spiracle and tongue-like lower calypteres. However, the lower calypteres of *Termitoloemus* differ strikingly from all rhinophorids in having a distinct notch at the posterior base (fig. 6). The lappet of the metathoracic spiracle is provided with stiff bristle-like hairs among the usual hairs. This condition is not found in the Rhinophoridae, but several groups of Calliphoridae possess stronger hairs on the anterior lappet.

I have investigated the slide-mounted genitalia of the male holotype of *T. marshalli*. The aedeagus is highly apomorphic and very unlike that of any rhinophorid (or any other tachinoid) and its ventral plates are not fused (Baranov, 1936: fig. 1). This evidence, indeed, does not

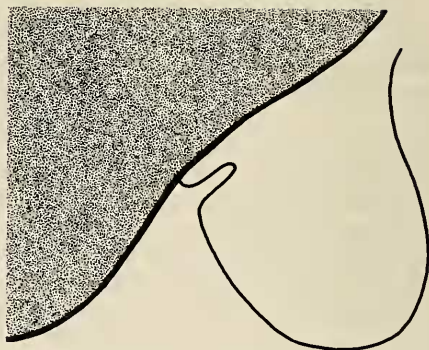


Fig. 6. *Termitoloemus marshalli* Baranov. Semidiagrammatical drawing of right lower calyptere of holotype ♂.

give much hint of the family affinity of *Termitoloemus*. The lower calypteres are not of the typical tongue-like rhinophorid type but more similar to the plesiomorphic, enlarged type, and the metathoracic spiracle can be taken as evidence for either a calliphorid or a rhinophorid status. I do not find a rhinophorid assignment the most corroborative and I have chosen to consider *Termitoloemus* to belong to the Calliphoridae.

Examined species: *Termitoloemus marshalli* Baranov, 1936.

An inventory of the genera accepted as Rhinophoridae in the present paper is given in table 2. Note that *Cirillia* is treated as a junior synonym of *Phyto*.

THE PHYLOGENY OF THE RHINOPHORID GENERA

Very few attempts to create a suprageneric classification of the Rhinophoridae have been made, and these are often of little utility owing to the inclusion of several non-rhinophorid genera.

Townsend (1935, 1938) divided his Melanophoridae (of which more than half of the genera were non-rhinophorids) into the five tribes Villeneuveiellini, Melanophorini, Acampominthoini, Eggisopsini, and Moriniini. Ségué (1941), still with a rather broad (sub)family concept, arranged the few genera of which he had investigated the male genitalia into four groups based on perceived similarity. In the first group, *Morinia* (as *Calobataemyia*) is placed with *Nyctia* Panzer (Sarcophagidae), as Ségué apparently has dissected a specimen of *Nyctia* erroneously taken for a *Morinia* specimen (see his fig. 445, p. 343). Two other groups, both monogeneric, contain *Stevenia* and *Melanomya* (as *Morinia*), and the last group consists of *Phyto*, *Rhinomo-*

Table 2. Inventory of genera accepted as Rhinophoridae in the present paper. Following each generic name is the number of species described at present (in brackets) and an indented list of species investigated in the present study.

Acompomintho Villeneuve, 1927 (1 sp.)

A. lobata Villeneuve, 1927

Azaisia Villeneuve, 1939 (2 spp.)

A. obscura (Villeneuve, 1939)

A. setitarsis Villeneuve, 1939

Baniassa Kugler, 1978 (2 spp.)

B. fascipennis Kugler, 1978

B. paucipila Pape, 1985

Bequaertiana Curran, 1929 (2 spp.)

B. argyriventris Curran, 1929

B. basilewskyi Peris, 1957

Callidesia Kugler, 1978 (1 sp.)

C. pictipennis Kugler, 1978

Comoromyia Crosskey, 1977 (1 sp.)

C. griseithorax Crosskey, 1977; not seen)

Macrotarsina Schiner, 1857 (1 sp.)

M. longimana (Eggers, 1856)

Melanomyoides Crosskey, 1977 (1 sp.)

M. capensis (Zumpt, 1959)

Melanophora Meigen, 1803 (2 spp.)

Melanophora rovalis (Linnaeus, 1758)

Metoplia Kugler, 1978 (1 sp.)

M. carbonaria Kugler, 1978

Oplisa Rondani, 1862 (5 spp.)

O. aterrima (Strobl, 1899)

O. pollinosa Kugler, 1978

O. tergestina (Schiner, 1862)

Parazamimus Verbeke, 1962 (1 sp.)

P. congolensis Verbeke, 1962

Paykullia Robineau-Desvoidy, 1830 (8 spp.)

P. brevicornis (Zetterstedt, 1844)

P. kugleri (Herting, 1961)

P. maculata (Fallén, 1820)

Phyto Robineau-Desvoidy, 1830 (22 spp.)

(*Cirillia* Rondani, 1856, syn. n.)

P. angustifrons (Rondani, 1856) comb. n.

P. cingulata (Zetterstedt, 1844)

P. discrepans Pandellé, 1896

P. melanocephala (Meigen, 1824)

P. pauciseta Herting, 1961

Queximyia Crosskey, 1977 (1 sp.)

Q. flavipes Crosskey, 1977

Rhinomorinia Brauer & Bergenstamm, 1889 (12 spp.)

R. capensis (Brauer & Bergenstamm, 1893)

R. sarcophagina (Schiner, 1862)

R. xanthocephala (Bezzi, 1908)

Rhinophora Robineau-Desvoidy, 1830 (1 sp.)

R. lepida (Meigen, 1824)

Stevenia Robineau-Desvoidy, 1830 (18 spp.)

S. angustifrons Villeneuve, 1913

S. atramentaria (Meigen, 1824)

S. deceptoria (Loew, 1847)

S. fernandezi Baez, 1978

S. hirtigena Herting, 1961

S. umbratica (Fallén, 1820)

Tricogena Rondani, 1856 (1 sp.)

T. rubricosa (Meigen, 1824)

Tromodesia Rondani, 1856 (2 spp.)

T. angustifrons Kugler, 1978

Ventrops Crosskey, 1977 (> 1 sp.)

V. milichioides Crosskey, 1977

V. spp. undescribed, Pape (in prep.)

rinia (as *Metopisena*), *Angioneura*, *Rhinophora*, and *Melanophora*.

Herting (1961), in his revision of the Palaearctic species, divided the (sub)family into two tribes: Azaisiini (containing *Azaisia* and *Acompomintho*), with long antennae and elongate second arisal segment, and the clearly paraphyletic Rhinophoriini, without these characters.

In the following is presented a phylogenetic analysis of the rhinophorid genera based on principles of phylogenetic systematics. Apomorphies (numbers refer to the cladogram, fig. 30) are only given for genera with more than one species, as autapomorphies of single species (if present) are not necessary for cladogram construction.

The species investigated are listed in table 2. As rhinophorids are sparse in museum collections, most of the species were seen in only few (1–5) specimens.

The monophyly of the Rhinophoridae, as de-

finied above, seems well corroborated by at least three synapomorphies:

- (1) cephalopharyngeal skeleton of first-stage larvae with toothed mandibles and an elongated pharyngeal sclerite,
- (2) parasites of woodlice,
- (3) distiphallus with well-developed ventral plates, which are fused along the ventral margins (secondarily free in *Paykullia*).

Two monophyletic subgroups, the *Phyto* group and the *Stevenia* group, can be erected on larval morphology, as previously discussed. The monophyly of the *Phyto* group is corroborated by the apomorphy:

- (4) eighth abdominal segment of first-stage larvae with terminal lobes, a dorsal tongue, and paired ventral ridges.

No shared apomorphic characters of the adult morphology have been found for the group, and as the first-stage larva is known for representatives of only three of the eight genera, the *Phyto* group is admittedly somewhat weakly founded.

The first split in the *Phyto* group separates *Paykullia* + (*Melanophora* + *Bequaertiana*) from the remaining genera, this group possessing the synapomorphies:

- (5) female terminalia of the reduced non-telescopic type,
- (6) wing cell r_{4+5} long petiolate.

Herting (1961) states that in the Palaearctic fauna only *Paykullia* and *Melanophora* possess shortened female terminalia (character 5), and Crosskey (1977), in his revision of the Afrotropical fauna, notes that the female terminalia of the Afrotropical species apparently is of the normal telescopic type, although he did not dissect any specimen.

Females of *Bequaertiana* are still unknown, but the assumed presence of non-telescopic terminalia seems well founded in the close affinity between *Melanophora* and *Bequaertiana*, as discussed below.

Character 6 is rather weak as the petiolate condition has arisen independently several times in the Rhinophoridae, and in *Bequaertiana* and *Melanophora asetosa* Kugler the bend of M is missing and an ancestral petiolate condition has to be assumed.

Paykullia is a well-defined genus with the following apomorphies:

- (7) distiphallus stout, possessing a strongly spinose pad on the ventral margin of each of the ventral plates and with the dorsal wall more or less prolonged (fig. 7),
- (8) male abdominal sternite 5 simple.

As most male calyptrates possess a more or less excavated abdominal sternite 5, the simple, almost rectangular shape in *Paykullia* must be an apomorphic character.

The monophyly of *Bequaertiana* + *Melanophora* is corroborated by the synapomorphies:

- (9) parafrontalia with several (about 4–7) proclinate orbital setae,
- (10) male antennae with characteristic bottle-brush-like hairing (Crosskey, 1977: figs. 17 and 27).
- (11) hind coxae elongated.

The hind coxae of *Bequaertiana* males (females still unknown) are distinctly elongated; in both sexes of *Melanophora roralis* they are only slightly so. In addition, *Bequaertiana* and *Melanophora* possess very similar distiphalli (figs. 8, 9).

The family affinities of *Bequaertiana* have been much discussed, Zumpt (1956) even suggesting an acalyptrate assignment. Crosskey (1977) doubts whether *Bequaertiana* is a rhino-

phorid and although he notes the resemblance of the head to that of *Melanophora roralis* he is more inclined to accept a relation to *Parazamimus*, another aberrant genus from the rainforests of Zaire. The striking agreement in the apomorphic structure of the male antennae, the head, and the hind coxae of both *Melanophora* and *Bequaertiana*, however, leaves no doubt of their close affinity. Actually a case can be made for treating them as congeners. *Melanophora asetosa*, of which only the female is known, seems to be a typical *Melanophora* (as judged from the description in Kugler (1978)) except for the absence of the bent part of vein M, which is an apomorphic character of *Bequaertiana*! In the collection of the Zoological Museum, University of Copenhagen, there is a single female *Melanophora* from Kenya, Naro Moru, likewise with the bend of vein M missing. The terminalia appear to be of the short non-telescopic type found in *Melanophora* and *Paykullia* (as seen in situ, the specimen is not dissected). On this evidence it seems most probable (with a parsimonious concept) that the reduced terminalia are a synapomorphy for the group *Paykullia* + (*Melanophora* + *Bequaertiana*).

The discovery of a female *Bequaertiana* and a male *Melanophora asetosa* may be most interesting, and if, as I think is most probable on the present evidence, the genus *Melanophora* is paraphyletic with respect to *Bequaertiana*, it will be necessary either to fit *Bequaertiana* into the generic limits of *Melanophora* or to place *M. asetosa* in the genus *Bequaertiana*.

Melanophora asetosa and *Bequaertiana* share the apomorphy:

- (12) bent part of vein M absent (Kugler, 1978: fig. 15; Crosskey, 1977: fig. 28).

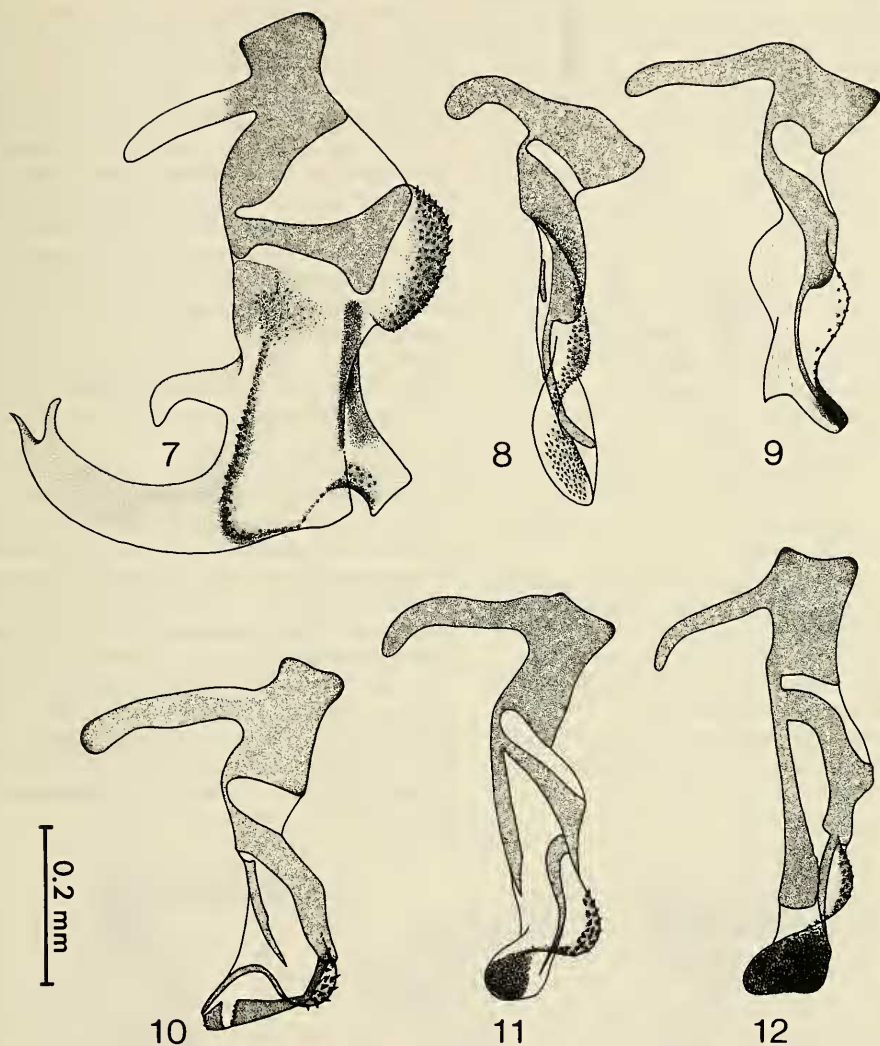
A similar wing venation occurs in *Oplisa aterrima* but is obviously a convergence.

The genus *Bequaertiana* possesses some remarkable autapomorphies:

- (13) tibiae in males without clearly differentiated bristles,
- (14) male abdomen covered with thick silvery pollinosity,
- (15) wing vein R_1 strongly haired along its length.

Melanophora (in the restricted sense with *M. roralis* as the only representative) is characterized by the distinctive white wing tips in females.

The sister group to *Paykullia* + (*Melanophora* + *Bequaertiana*) is somewhat ill-defined and



Figs. 7—12. Aedeagus of Rhinophoridae, lateral view: 7, *Paykullia maculata* (Fallén). 8, *Melanophora roralis* (Linnaeus). 9, *Bequaertiana argyri-ventris* Curran. 10, *Callidesia pictipennis* Kugler. 11, *Tromodesia angustifrons* Kugler. 12, *Baniassa fascipennis* Kugler.

may be polyphyletic. The possible monophyly of the group is corroborated by the single synapomorphy:

(16) surstylar base extended medially (fig. 13).

This may seem very conclusive, but several exceptions are found. The median extension is absent in *Phyto pauciseta* and both species of *Baniassa*, and indistinct in *Phyto angustifrons*. The first split in this group separates *Tromodesia* + *Callidesia* from the remaining genera, their monophyly being corroborated by the synapomorphies:

(17) clypeus distinctly bulging,

(18) distiphallus of characteristic shape with the sclerotization of the spermduct bent dorsally (figs. 10, 11).

The two genera are depicted as sister groups on the cladogram (fig. 30), but they are very similar and could as well be treated as a single genus. I have not seen any specimen of *Tromodesia vibripennis* Rondani, the type species of *Tromodesia*, and therefore I have not been able to evaluate the monophyly of the genus, i.e., to investigate whether *T. vibripennis* is more

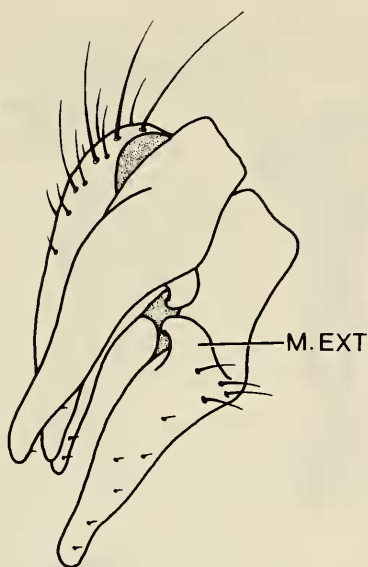


Fig. 13. *Phyto melanocephala* (Meigen). Cerci and surstyli, ventrolateral view, showing median extensions (m.ext) of surstyli.

closely related to *T. angustifrons* than to any other species (or species group).

The monophyly of the sister group of *Tromodesia* + *Callidesia* seems well corroborated by the apomorphies:

(19) lunula with setae,

(20) notopleuron haired in addition to the usual two bristles,

(21) katepimeron haired.

All these traits occur sporadically in other rhinophorids, viz., many species of *Paykullia* and *Rhinophora lepida* possess some lunular setae; *Tricogena*, some *Stevenia*, and *Rhinomorinia sarcophagina* may have a few additional notopleural hairs; and some *Rhinomorinia* may have an occasional hair on the katepimeron (barette). However, the combination of these traits seems to have arisen only once in the Rhinophoridae.

Baniassa is the possible sister group of *Phyto* and is well characterized by the apomorphies:

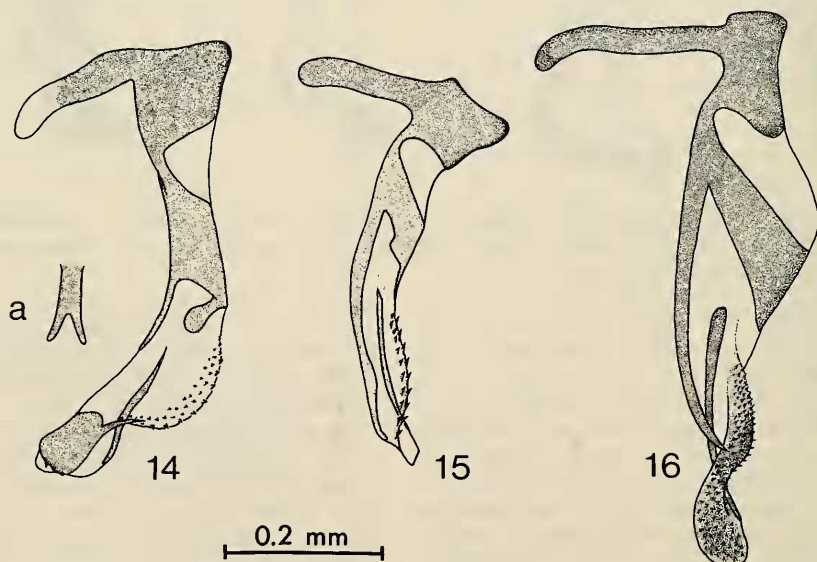
(22) strongly holoptic eyes in males,

(23) wings darkened apically,

(24) wing cell r_{4+5} petiolate,

(25) metathoracic spiracle with operculum.

As no other rhinophorids possess opercular metathoracic spiracles (character 25) this may be considered a reversal to the plesiomorphic condition. *Baniassa paucipila* Pape does not possess any of the synapomorphies 19—21 corroborating the monophyly of *Baniassa* + *Phyto*. However, the reduced hairing of *Baniassa paucipila* may be secondarily correlated with the yellow colouration of the thorax. Many yellow forms, e.g., the totally yellow species of *Parazamimus* and *Bequaertiana* from the rainforests of central Africa, possess a deviating, often re-



Figs. 14—16. Aedeagus of Rhinophoridae, lateral view. 14, *Parazamimus congolensis* Verbeke; a = dorsal sclerotization, dorsal view. 15, *Phyto angustifrons* (Rondani). 16, *Phyto melanocephala* (Meigen).

duced, hairing. This may be correlated with an association to a humid habitat.

The aedeagus of *B. fascipennis* is shown in fig. 12.

Phyto (including *Cirillia*) possesses the apomorphies:

(26) sclerotization of the spermduct interrupted (figs. 15, 16),

(27) strong pre-alar bristle.

Cirillia is characterized by the strongly developed parafacial setae and a long-petiolate wing cell r_{4+5} . These characters are likewise found in many species of *Phyto*, e.g., *P. hertingi* Baez, and as *Phyto* does not possess any derived characters not shared with *Cirillia*, a generic separation between these seems unnatural in a phylogenetic sense.

Parazamimus is a strange monotypic genus from the tropical rainforests of Zaire. The single specimen known is in somewhat bad condition and the micropin, by which the head is mounted on the body, unfortunately penetrates the lunula, making it impossible to see whether setae are present. The structure of the distiphallus with the reduced sclerotization of the spermduct (fig. 14) is very reminiscent of *Phyto*, and *Parazamimus* is tentatively placed as a sister group to *Phyto* although it does not possess any of the synapomorphies given for *Baniassa* + *Phyto*.

Returning to the other group that could be erected on larval morphology, the *Stevenia* group, the possible monophyly is corroborated by the apomorphies:

(28) setal bases of first-stage larvae produced into proleg-like structures,

(29) acrophallus sclerotized and tripartite.

Other genera like *Parazamimus* and *Tromodesia* have the acrophallus partly sclerotized, but apparently developed independently and without the tripartition which is so characteristic of the *Stevenia* group. Typically the acrophallus is divided into two lateral and one ventral sclerotization (the latter being the extension of the spermduct sclerotization), but often a dorsal acrophallic sclerite is more or less distinct. In some genera this dorsal sclerite is simple but in others it is provided with two lateral armlike processes. The three acrophallic sclerites are more or less grooved and probably guide the sperm into the ducts of the female seminal receptacles; a functional analogue to the acrophallus of many Tachinidae and Sarcophagidae (for the latter see Lopes, 1966; Lopes & Kano, 1968).

The first split in the *Stevenia* group separates

Melanomyoides, *Queximya*, *Rhinomorinia*, *Rhinophora*, and *Ventrops* from the remaining members of the group. All five genera have a general *Rhinomorinia*-like appearance and their monophyly is corroborated by the synapomorphy:

(30) dorsolateral processes of distiphallus fused into a single median sclerotization (fig. 22a).

Queximya is a monotypic genus from South Africa, easily recognized by the very long antennae and characteristic head profile (Crosskey, 1977: fig. 14). The possession of a strong pre-alar bristle suggests an affinity with *Phyto*, but a bare katepimeron, the lack of lunular setae, and the fusion of the dorsolateral processes of the distiphallus suggest this to be unlikely. The long antennae could be taken as evidence for a close affinity to either *Azaisia* or *Acompintho*, but no other characters support this position and the present assignment based on the aedeagal structure (fig. 18) seems the best corroborative.

Ventrops is another well-defined Afrotropical genus, at present with only a single described species, but other species are known. The aedeagus of *V. milichioides* is shown in fig. 17. *Ventrops* possesses the following apomorphies:

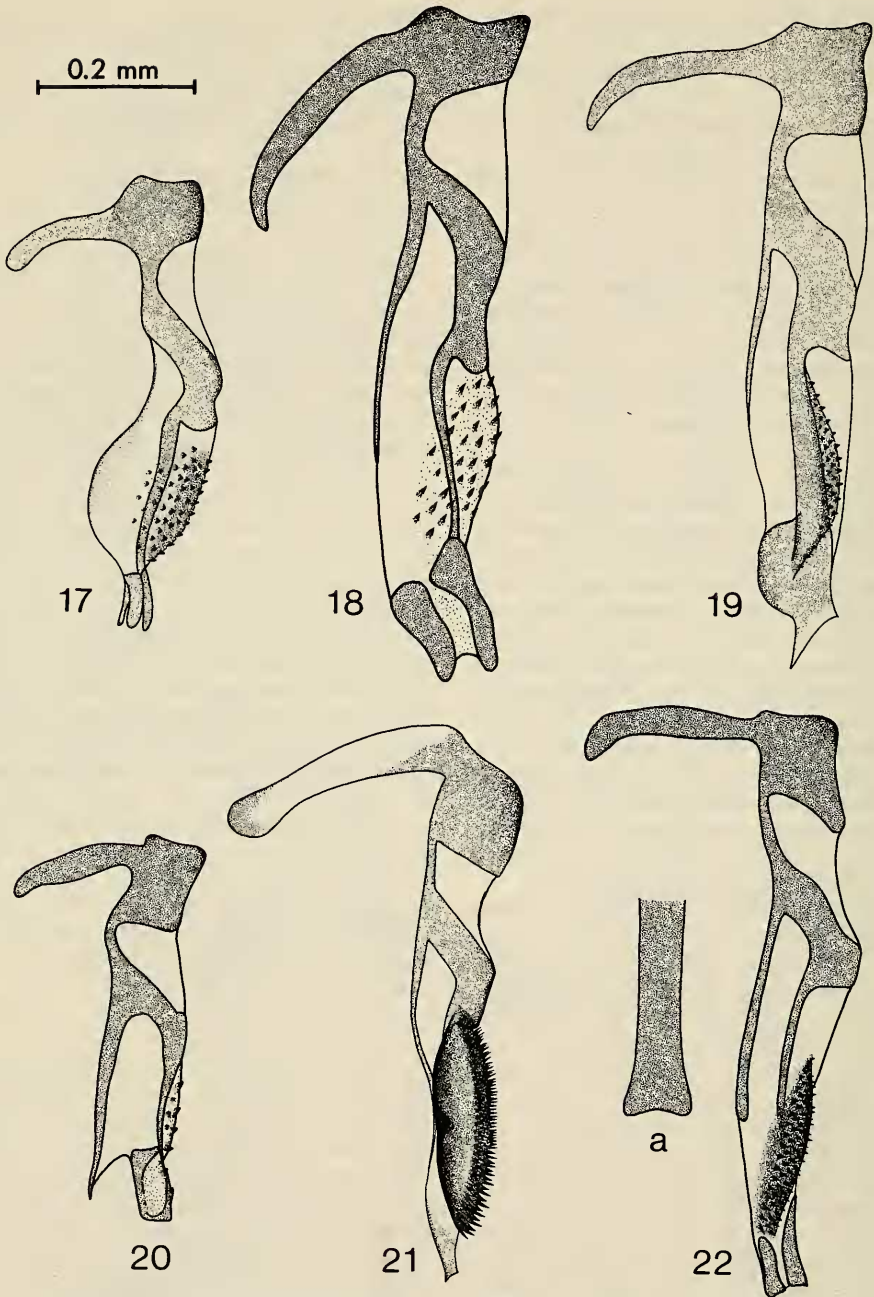
(31) eyes greatly enlarged, occupying most of the side of the head and with a concave hind margin (Crosskey, 1977: fig. 13),

(32) cerci very short and almost concealed between the surstylar bases.

The remaining three genera, *Melanomyoides*, *Rhinomorinia*, and *Rhinophora* seem to comprise a monophyletic group corroborated by their apomorphic head structure:

(33) epistome strongly warped forwards (Crosskey, 1977: figs. 8—10, 12)

Melanomyoides is a monotypic genus, its representative *M. capensis* being originally described as a species of *Chaetostevenia* Brauer (= *Paykullia*) by Zumpt (1959). Crosskey (1977) discusses the affinity of *Melanomyoides* to other (supposed) rhinophorid genera, and mentions an extreme superficial similarity to *Melanomya* and an even closer resemblance to *Angioneura*. These similarities, however, are founded in all three genera being composed of small, shining black flies with holoptic eyes in the male, characters which are not especially convincing; Crosskey concludes by stressing the resemblance in head profile and distiphallus between *Melanomyoides* and *Rhinomorinia*. Similarly, a case could be made for a sister



Figs. 17—22. Aedeagus of Rhinophoridae, lateral view: 17, *Ventrops milichioides* Crosskey. 18, *Queximya flavipes* Crosskey. 19, *Rhinophora lepida* (Meigen). 20, *Melanomyoides capensis* (Zumpt). 21, *Rhinomorinia xanthocephala* (Bezzi). 22, *Rhinomorinia sarcophagina* (Schiner); a = dorsal sclerotization, dorsal view.

group relation between *Melanomyoides* and *Rhinophora*, both having somewhat similar wings with a petiolate cell r_{4+5} , but a very short petiole occurs in some Afrotropical *Rhinomorinia*. *Melanomyoides* is easily distinguished by the almost leaflike surstyli, the holoptic male eyes, and the petiolate wing cell r_{4+5} . The aedeagus of *M. capensis* is shown in fig. 20.

Rhinophora is likewise monotypic and is easily separated from *Melanomyoides* by the dichoptic eyes in males and the presence of lunar setae. The aedeagus is shown in fig. 19.

The genus *Rhinomorinia* is difficult to characterize on external adult morphology and I have only found a single character which may establish the monophyly of the genus:

(34) Distiphallus ventrally with a greatly enlarged spinous surface (figs. 21, 22).

The long and slender cerci and surstyli (Crosskey, 1977: figs. 34, 35) may be another character, but a very similar condition is seen in *Queximya*.

The sister group to the four *Rhinomorinia*-like genera possesses the following apomorphies:

(35) acrophallus more complex, the sclerites

being longer and more distinctly grooved, (36) dorsal wall of distiphallus extended.

A dorsal extension is likewise found in *Melanomyoides* (fig. 20) but this is probably a convergence.

Two other characters which may be synapomorphies for this group are:

(37) dorsal acrophallic sclerite well-developed, with two lateral arms,

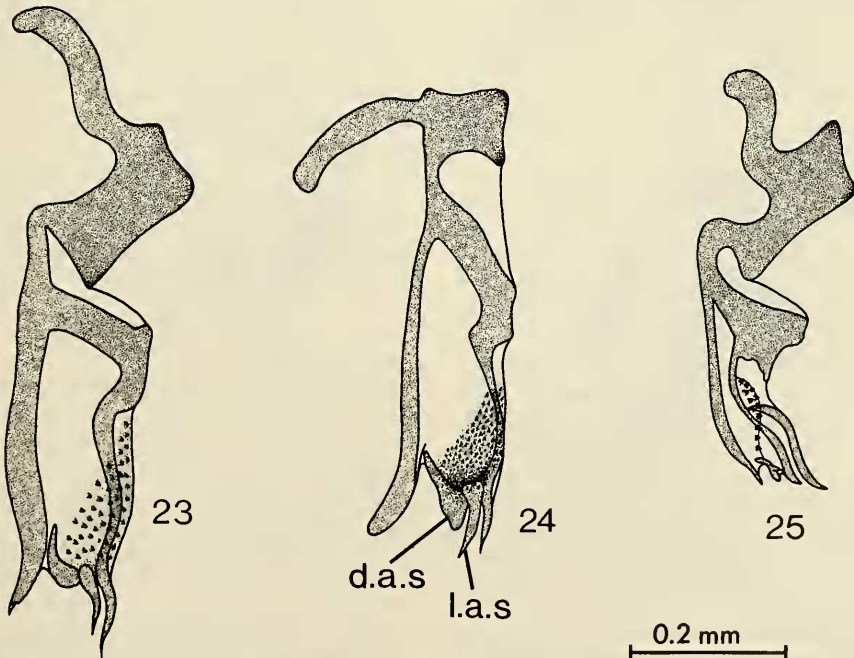
(38) hypandrium spoon-shaped.

Character 37, however, is not found in *Metoplisia*, most *Oplisa* and most *Stevenia*. Character 38 is especially distinct in *Tricogena*, *Oplisa*, *Metoplisia*, and *Azaizia*, and the flat hypandrium found in *Stevenia* must be secondarily derived.

The first split in this group separates *Acompomintho* + (*Azaizia* + *Macrotarsina*) from the others. The monophyly of these three genera is corroborated by the following synapomorphy:

(39) anal vein (A_1) shortened.

Acompomintho, the only genus endemic to the Oriental Region, is well defined by the long antennae with prolonged second arisal segment, the well-developed parafacial setae (Lopes, 1938: pl. 1, fig. 2) and the long-petiolate wing cell r_{4+5} . The aedeagus is shown in fig. 25.



Figs. 23—25. Aedeagus of Rhinophoridae, lateral view: 23, *Macrotarsina longimana* (Eggers). 24, *Azaizia obscura* (Villeneuve). 25, *Acompomintho lobata* Villeneuve. Abbreviations: d.a.s = dorsal acrophallic sclerite; l.a.s = lateral acrophallic sclerite.

Azaisia + *Macrotarsina* possess the synapomorphies:

- (40) anterior katepimeral bristle much weaker than posterior one,
- (41) dorsal acrophallic sclerite well-developed, other acrophallic sclerites slender and situated close together (figs. 23, 24),
- (42) gonopods (pregonites) thickened (only slightly in *Azaisia*).

In *Acompomintho* (and all other rhinophorids) the two katepisternal (sternopleural) bristles (character 40) are subequal to equal in size.

Macrotarsina is well characterized by the greatly prolonged male fore tarsi. *Azaisia* is more difficult to characterize; the most conspicuous trait, which may be autapomorphic for *Azaisia*, is:

- (43) antennae long, with prolonged second arisal segment.

This character is likewise found in *Acompomintho* and may actually indicate a sister group relation between *Acompomintho* and *Azaisia* as accepted by Herting (1961), who established a separate tribe containing these two genera. However, I consider the sister group relation between *Azaisia* and *Macrotarsina* to be more corroborated by the present evidence.

The monophyly of the sister group of *Acompomintho* + (*Azaisia* + *Macrotarsina*) is corroborated by the apomorphy:

- (44) ventral plates of aedeagus with a pair of processes, each supporting a spinous pad (figs. 26—29).

The first split in this group separates *Metoplisia* from *Oplisa* + (*Stevenia* + *Tricogena*). Kugler (1978), in his description of *Metoplisia carbonaria*, mentioned the superficial similarity to *Oplisa*, but he erected the genus because the three humeral bristles of *Metoplisia* form an obtuse-angled triangle and not an almost right-angled triangle as in *Oplisa*. The latter configuration is used as a key character for the genus *Oplisa* by Herting (1961) and Kugler (1978), but both *Stevenia* (with *S. hirtigena* as an exception) and *Tricogena* possess this character. As no other rhinophorids possess this arrangement of the humeral bristles, and as the arrangement in an obtuse-angled triangle is of widespread occurrence, the almost right-angled configuration is assumed to be a synapomorphy for *Stevenia*, *Tricogena*, and *Oplisa*:

- (45) three humeral bristles forming an almost right-angled triangle.

Oplisa was divided by Herting (1961) into the two subgenera *Oplisa* (as *Hoplisa*) sensu stricto,

characterized by latero-reclinate ocellar bristles, and the monotypic *Anoplisa* with proclinate ocellar bristles. Kugler (1978) described two additional species of *Oplisa*, which both would fall into the subgenus *Anoplisa*, but as this is clearly a paraphyletic group (as defined by Herting) it is not accepted in the present paper.

Oplisa is somewhat difficult to characterize by distinct autapomorphies. The enormously enlarged ejaculatory sclerite of *O. tergestina*, *O. aterrima*, and *O. oldenbergi* (Herting) (see Crosskey, 1977: fig. 40; Draber-Moňko, 1978: fig. 18) is unique in the Rhinophoridae, but *O. pollinosa* possesses a normal-sized ejaculatory sclerite.

The following apomorphies corroborate the monophyly of *Oplisa*:

- (46) distiphallus with the processes of the ventral plate, which support the spinous pads, situated on a stalked extension (fig. 27),
- (47) male cerci short and blunt, not separated apically,
- (48) surstyli broadened apically.

It seems fairly corroborated that a sister group relation exists between *Stevenia* and *Tricogena*, which share the apomorphy:

- (49) parafacial plate with a row of strong setae.

Both genera are very similar in external morphology and in the structure of the aedeagus (figs. 28, 29). *Stevenia* is a well-defined genus with the following apomorphies:

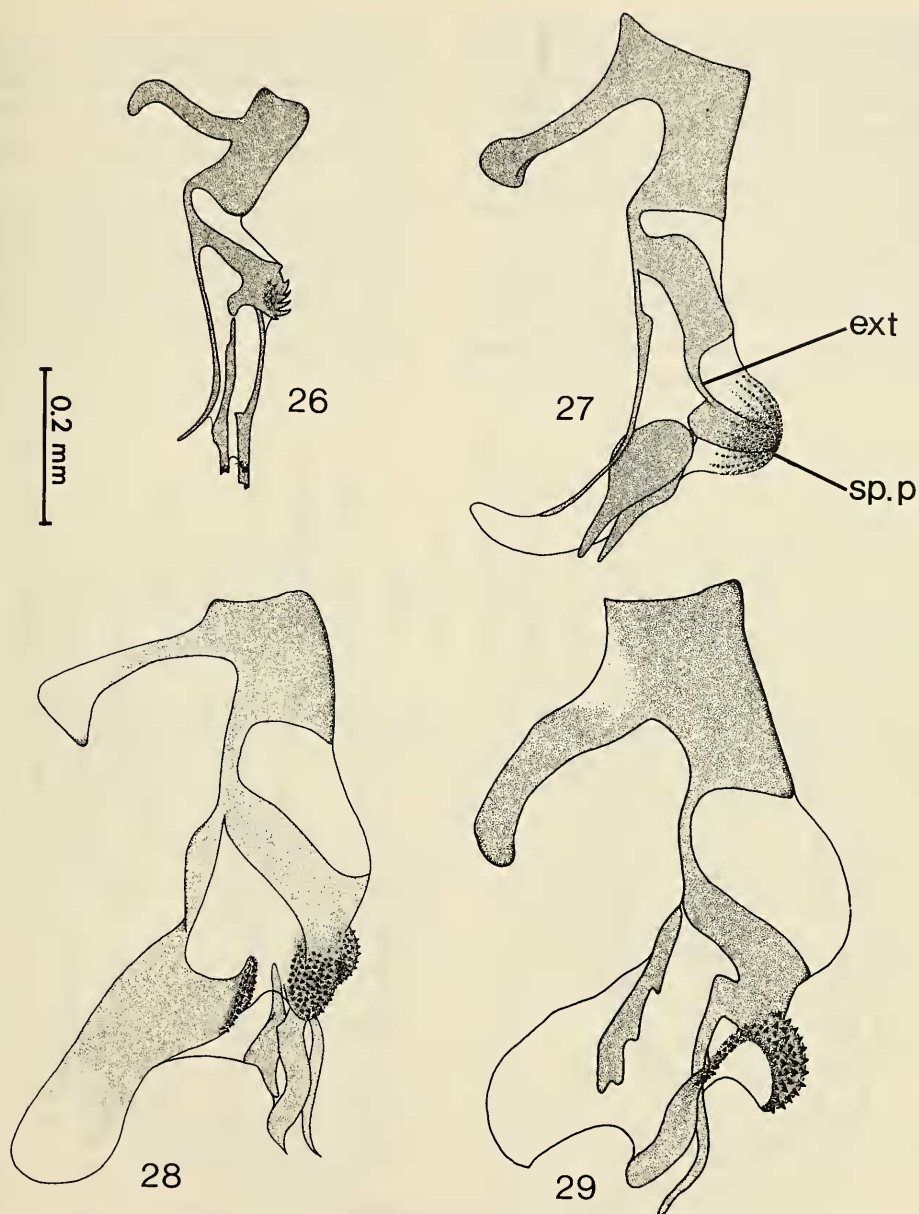
- (50) wing cell r_{4+5} petiolate,
- (51) hypandrium flat,
- (52) mid femur in males with a posteroventral comb of short stout bristles apically.

Some species do not, however, possess character 52 (Herting, 1961), which may define an infrageneric subgroup.

GENUS INCERTAE SEDIS

Comoromyia Crosskey.

Crosskey (1977) described the genus on a single female of *C. griseithorax*. I have not seen this specimen, which seems to be the only one known at present, and I have not been able to incorporate the genus into the cladogram on the basis of the description alone. Crosskey mentions a possible relationship with *Phyto*, as *Comoromyia* possesses a strong pre-alar bristle, but the bare katepimeron weakens this argument. I prefer to exclude *Comoromyia* from the cladogram (fig. 30) until more information is available, especially with regard to the structure of the aedeagus as this provides several of the set-defining characters of the present analysis.



Figs. 26—29. Aedeagus of Rhinophoridae, lateral view: 26, *Metoplis carbonaria* Kugler. 27, *Oplisa aterrima* (Strobl). 28, *Tricogena rubricosa* (Meigen). 29, *Stevenia atramentaria* (Meigen). Abbreviations: ext = stalked extension of ventral plate; sp.p = spinous pad.

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Note added while this paper was already in press:

The paper by H.-P. Tschorsnig, 1985, Die Struktur des männlichen Postabdomens der Rhinophoridae (Diptera), Stuttg. Beitr. Naturk. ser. A 375, pp. 1—18, appeared after submitting this paper for publication and a detailed discussion of the hypotheses presented will appear in a future paper.

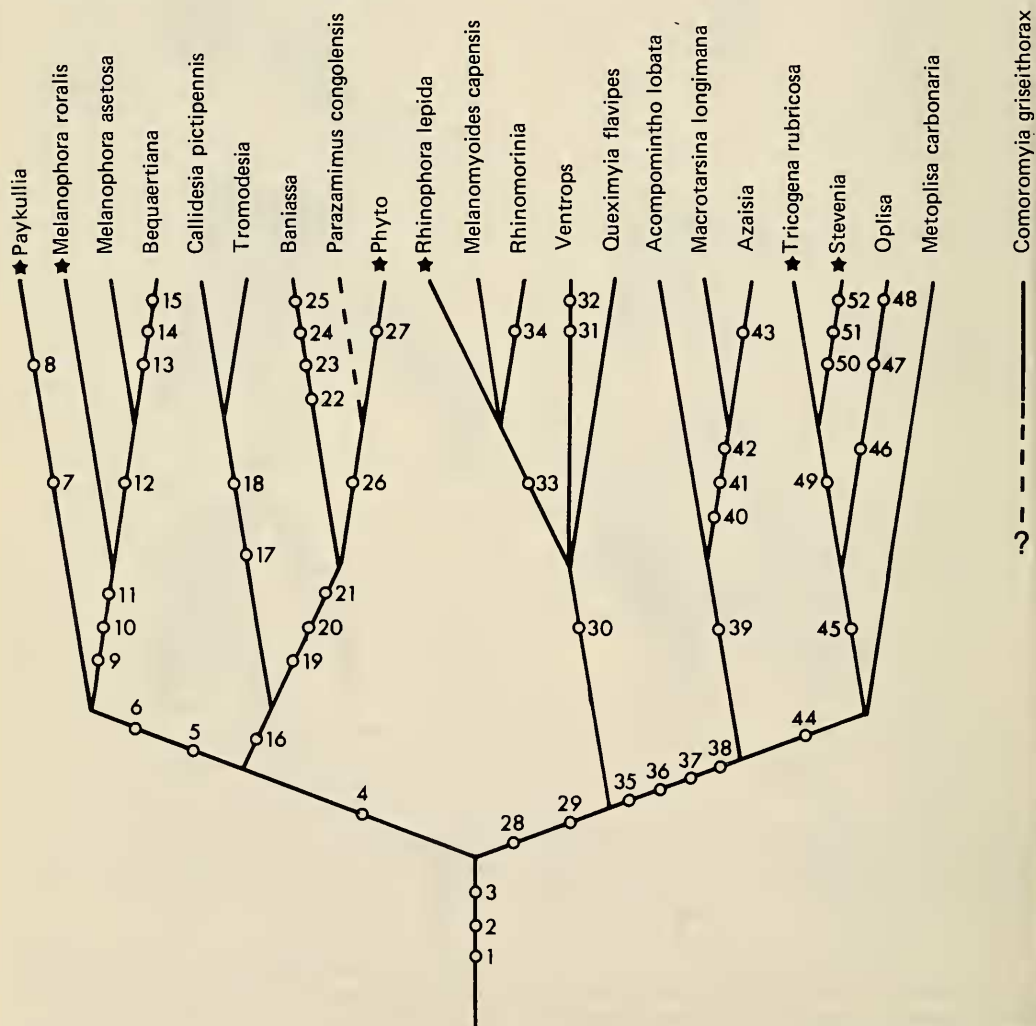


Fig. 30. Cladogram of the Rhinophoridae at the generic level. Numbers refer to apomorphies discussed in the text. Genera recorded as woodlouse parasites are marked with an asterisk.

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